
ADAPTIVE RADIATION OF THE HAWAIIAN SILVERSWORD ALLIANCE (COMPOSITAE–MADIINAE): ECOLOGICAL, MORPHOLOGICAL, AND PHYSIOLOGICAL DIVERSITY¹

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ABSTRACT

The ecological, morphological, and physiological diversity of species in the Hawaiian silversword alliance is exceptional. The 28 species, which belong to the endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia*, have a wide variety of geographical distributions and elevational ranges within the archipelago. They grow in habitats as varied as dry scrub and woodland, wet scrub and forest, cinder and lava, and bog. Ecological diversity is also evident among sympatric species. At a site of sympatry on the island of Hawaii, for example, *D. ciliolata* and *D. scabra* are restricted to different lava flows, even though individuals of the two species may grow within a meter of one another. The 28 species have growth forms as varied as rosette shrubs, shrubs, trees, and lianas. They have a wide range of leaf sizes and shapes, with the *Dubautia* species exhibiting significant variation in leaf turgor maintenance capacities. Morphological and physiological diversity is also evident among sympatric species. At a site of sympatry on the island of Maui, for example, *A. sandwicense* and *D. menziesii* exhibit different suites of morphological and physiological traits enabling them to cope with the severe environmental conditions. The patterns of diversity and the genomic relationships among the 28 species suggest that a variety of factors may have played important roles in their adaptive radiation.

The Hawaiian silversword alliance is a premier example of adaptive radiation in plants (Carlquist, 1980; Carr et al., 1989). The alliance includes 28 species in three endemic genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia* (Carr, 1985). The species grow in a wide range of habitats and have a wide variety of growth forms. They are also closely related, as evidenced by the high frequency of spontaneous interspecific and intergeneric hybrids in nature, coupled with the ease of production of artificial hybrids in the laboratory (Carr & Kyhos, 1981, 1986). The detailed analysis of the hybrids and parental taxa using cytogenetic, electrophoretic, and molecular approaches has provided compelling evidence that the silversword alliance is a genetically cohesive group whose origin and di-

versification probably trace to a single colonizing ancestor (Baldwin et al., 1988; Carr et al., 1989).

Our objective in this review is to provide insight into the ecological, morphological, and physiological diversity of species in the silversword alliance. With respect to ecological diversity, we compare the geographical distributions, habitats, and elevational ranges of the 28 species, then analyze the local distributions of several sympatric *Dubautia* species. With respect to morphological and physiological diversity, we compare the growth forms, leaf sizes, and leaf shapes of the 28 species, then examine the turgor maintenance capacities of the *Dubautia* species and the water and temperature balances of two sympatric *Argyroxiphium* and *Dubautia* species. Our primary theme is that the

¹ This paper is dedicated to Dr. Sherwin Carlquist in honor of his pioneering research on the Hawaiian silversword alliance. The research was supported by NSF Grant DEB-8206411 and a gift from the Atlantic Richfield Foundation to the senior author. We thank Lani Stemmermann for invaluable companionship, botanical insight, and technical assistance in the field. We also thank the staff of Haleakala National Park, particularly R. Nagata and L. Loope, for critical logistical support, and J. Canfield and N. Friedman for generous photographic assistance.

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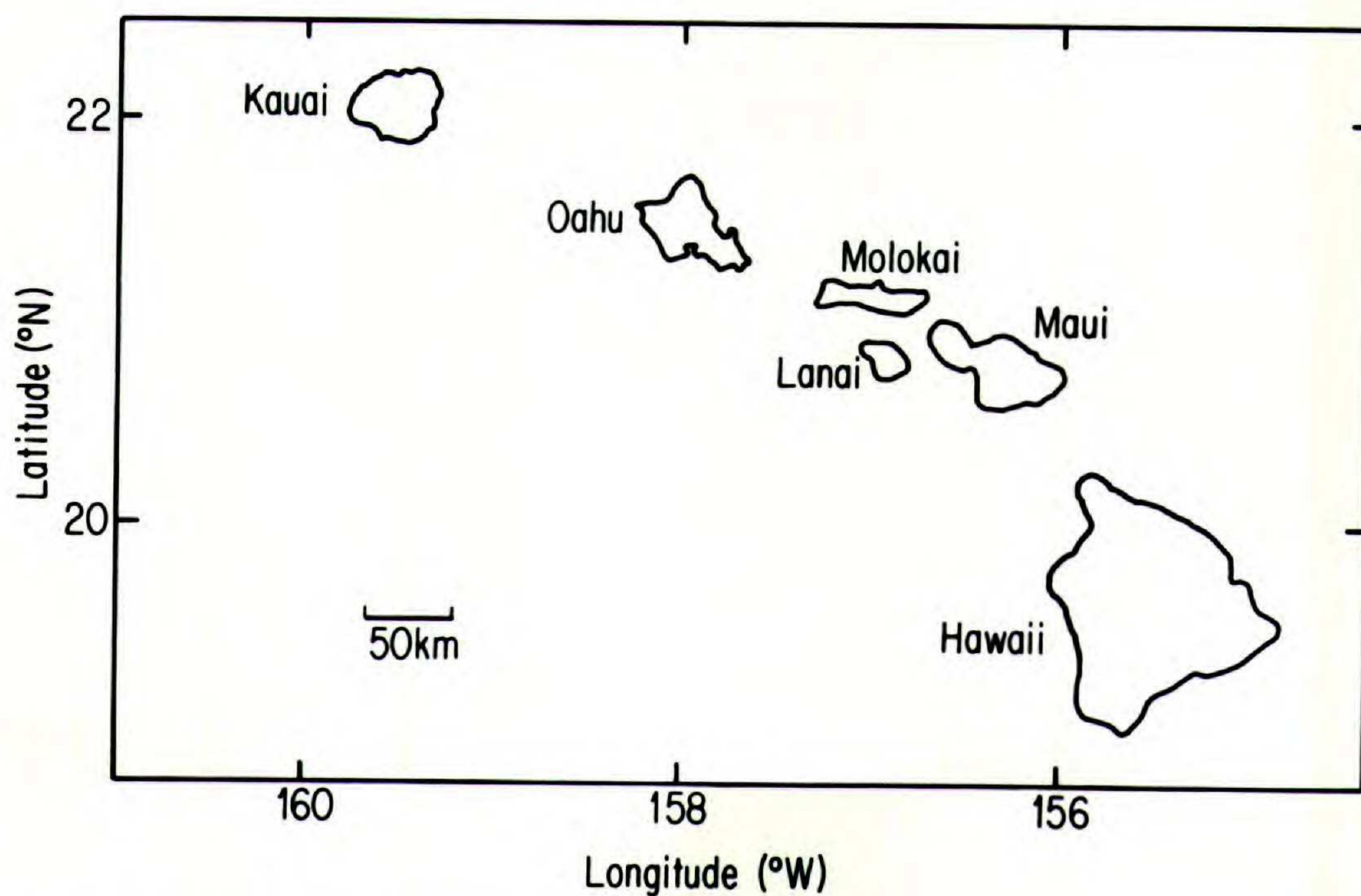


FIGURE 1. Major islands of the Hawaiian archipelago.

ecological, morphological, and physiological diversity of the species is exceptional. Understanding the pattern and significance of this diversity, together with the factors giving rise to it, provides a key to understanding adaptive radiation in plants.

ECOLOGICAL DIVERSITY

The Hawaiian archipelago includes six major islands (Fig. 1). Maui, Lanai, and Molokai, which are currently separated by shallow channels, were united into one large island during periods of lower sea level in the Pleistocene (Macdonald & Abbott, 1970). Thus, they function as a single biogeographic unit known as the Maui complex (Carson & Kaneshiro, 1976; Simon, 1987). The ages of the islands increase progressively from southeast to northwest. Based on potassium-argon dating, the ages of older sections of the islands, in millions of years, are: Hawaii—0.7, Maui—1.3, Lanai—1.5, Molokai—1.8, Oahu—3.3, and Kauai—5.6 (Macdonald & Abbott, 1970).

Species in the silversword alliance have significantly different geographical distributions within the archipelago (Table 1). All *Argyroxiphium* species, most 13-paired *Dubautia* species, and one 14-paired *Dubautia* species are confined to Hawaii, the Maui complex, or both. Most 14-paired *Dubautia* species and both *Wilkesia* species, in contrast, are confined to Kauai. Two 13-paired *Dubautia* species are restricted to Oahu, and two 14-paired species grow on Kauai, Oahu, and at least one of the younger islands. Of the latter species, only *D. plantaginea* grows on all major islands.

The archipelago supports a wide variety of terrestrial habitats. The habitats containing species in the silversword alliance are grouped into four broad categories in Table 1. The dry scrub and woodland habitat has low annual rainfall with a prolonged dry season. The vegetation ranges from low, open scrub dominated by deciduous and evergreen shrubs to taller woodland with scattered deciduous and evergreen trees. The wet scrub and forest habitat has medium to high annual rainfall without a prolonged dry season. The vegetation ranges from tall, closed forest with a high diversity of evergreen trees to lower, more open forest and scrub dominated by the evergreen *Metrosideros polymorpha* (Myrtaceae) and rich in epiphytic bryophytes and pteridophytes. The bog habitat has very high annual rainfall, waterlogged, acidic soils, and stunted vegetation. The cinder and lava habitat has low or high annual rainfall, exposed volcanic substrates with very limited soil development, and sparse vegetation. The range in annual rainfall among the four habitats, from less than 400 mm to more than 12,300 mm, is exceptional.

Species in the silversword alliance have significantly different distributions among the four habitats (Table 1). One *Argyroxiphium* species, six 13-paired *Dubautia* species, and both *Wilkesia* species grow in the dry scrub and woodland habitat. Most *Argyroxiphium* species, four 13-paired *Dubautia* species, and all 14-paired *Dubautia* species, in contrast, grow in the wet scrub and forest habitat, the bog habitat, or both. In addition to growing in other habitats, five species grow in the cinder and lava habitat, where they are among the first

TABLE 1. Ecological and morphological characteristics of *Argyroxiphium*, *Dubautia*, and *Wilkesia* species. Nomenclature and diploid chromosome pairs derive from Carr (1985). Ecological and morphological data derive from the analysis of approximately 2,000 herbarium specimens (Carr, 1985) and from extensive field research. Islands are: H = Hawaii, K = Kauai, M = Maui complex, and O = Oahu. Habitats are: b = bog, c = cinder and lava, d = dry scrub and woodland, and w = wet scrub and forest. Growth forms are: l = liana, r = rosette shrub, s = shrub, and t = tree. Leaf lengths are ranges for mature leaves from dried specimens.

Species	Chromosome pairs	Island	Habitat	Elevational range (m)	Growth form	Leaf length (mm)
<i>Argyroxiphium caliginis</i>	14	M	b	1,350–1,650	r	35–150
<i>A. grayanum</i>	14	M	b	1,200–2,050	r	50–310
<i>A. kauense</i>	14	H	b	1,625–1,900	r	200–400
<i>A. sandwicense</i>	14	H, M	d, c	2,125–3,750	r	130–390
<i>A. virescens</i>	—	M	w	1,600–2,300	r	170–300
<i>Dubautia arborea</i>	13	H	d	2,125–3,100	s, t	30–90
<i>D. ciliolata</i>	13	H	d, c	900–3,200	s	5–30
<i>D. dolosa</i>	13	M	w	1,525–2,275	s	40–120
<i>D. herbstobatae</i>	13	O	d	580–925	s	20–55
<i>D. linearis</i>	13	H, M	d, w, c	450–2,500	s	10–75
<i>D. menziesii</i>	13	M	d, c	1,800–3,075	s	20–50
<i>D. platyphylla</i>	13	M	d	1,725–2,750	s	40–90
<i>D. reticulata</i>	13	M	w	1,575–2,300	s, t	30–70
<i>D. sherffiana</i>	13	O	w	600–1,150	s	25–100
<i>D. imbricata</i>	14	K	w, b	700–1,550	s	60–150
<i>D. knudsenii</i>	14	K	w	550–1,375	s, t	50–220
<i>D. laevigata</i>	14	K	w	575–1,250	s	70–240
<i>D. latifolia</i>	14	K	w	975–1,200	l	80–170
<i>D. laxa</i>	14	M, O, K	w, b	350–1,700	s	40–200
<i>D. microcephala</i>	14	K	w	825–1,275	s	100–240
<i>D. paleata</i>	14	K	b	1,100–1,550	s	35–200
<i>D. pauciflorula</i>	14	K	w	700–725	s	80–210
<i>D. plantaginea</i>	14	H, M, O, K	w	300–2,100	s	80–260
<i>D. raillardoides</i>	14	K	w	600–1,375	s	90–250
<i>D. scabra</i>	14	H, M	w, c	75–2,500	s	10–90
<i>D. waialealae</i>	14	K	b	1,450–1,600	s	10–30
<i>Wilkesia gymnoxiphium</i>	14	K	d	425–1,100	r	150–500
<i>W. hobdyi</i>	14	K	d	275–400	r	100–200

vascular plants to colonize the exposed volcanic substrates. The most widespread species ecologically is the 13-paired *D. linearis*, which grows in the dry scrub and woodland habitat, the wet scrub and forest habitat, and the cinder and lava habitat.

Elevations in the archipelago extend from sea level to 4,206 m (Mueller-Dombois, 1981). Species in the silversword alliance collectively span most of this elevational gradient, growing from 75 m to 3,750 m. The species have a wide variety of elevational ranges, however, with no two species having the same range (Table 1). *Dubautia pauciflorula* and *D. waialealae*, for example, have narrow ranges, whereas *D. ciliolata* and *D. scabra* have wide ranges. In addition, *D. herbstobatae* and *W. hobdyi* have ranges restricted to low elevations, whereas *A. sandwicense* and *D. arborea*

have ranges restricted to high elevations. At low elevations minimal daily temperatures rarely drop below 15°C. At high elevations, in contrast, minimal daily temperatures may drop below 0°C for extended periods, especially during winter months.

At many localities in the archipelago, species in the silversword alliance grow sympatrically. In several instances, the sympatric species exhibit local distributions that differ markedly. *Dubautia ciliolata* and *D. scabra*, for example, grow sympatrically at a site on the upper slopes of Mauna Loa, Hawaii. The site is covered by exposed lava from past eruptions of Mauna Loa. Most of the site is covered by pahoehoe lava from a 1935 eruption. This younger flow is discontinuous in places, however, such that lava from a prehistoric flow is exposed. The older flow consists of a mixture

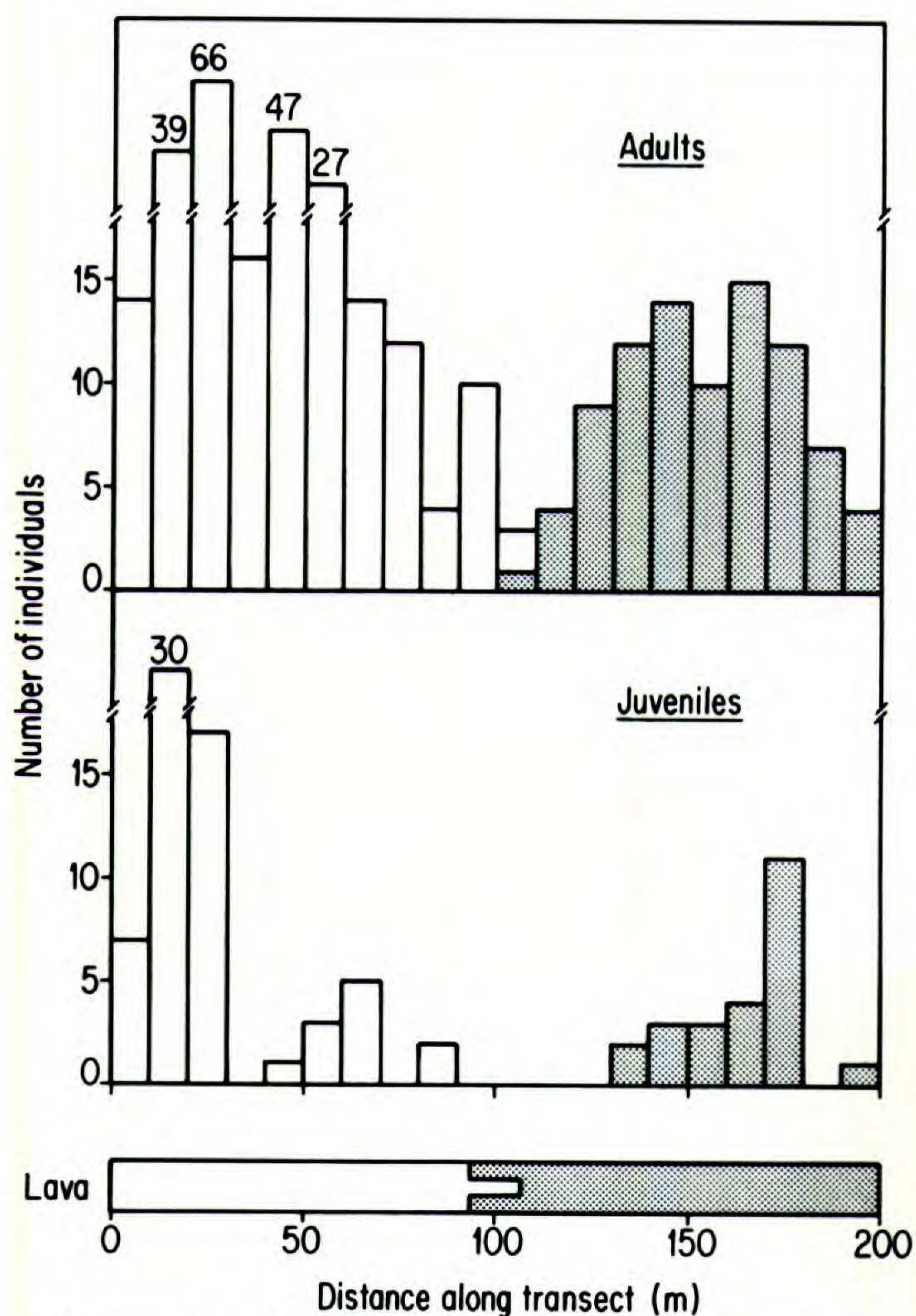


FIGURE 2. Distributions of adults and juveniles of *Dubautia ciliolata* and *D. scabra* at a site of sympatry on Mauna Loa, Hawaii. The site was located at 1,980 m near Puu Huluhulu along the Saddle Road (Robichaux, 1984). The 200-m-long, 10-m-wide transect crossed two lava flows. The first 100 m crossed an older flow of pahoehoe and aa lava; the second 100 m crossed a younger flow of pahoehoe lava. In the zone of interdigitation at 95–105 m, fingers of the younger flow covered sections of the older flow. At points of contact in this zone, the transition from one flow to the other was very abrupt. Adults and juveniles were defined as individuals with crown diameters greater than and less than 20 mm, respectively. In both species, large adults had crown diameters exceeding 1 m. For the number of individuals along the transect, the unshaded and shaded bars denote *D. ciliolata* and *D. scabra*, respectively. For the distribution of lava along the transect, the unshaded and shaded sections denote the older and younger flows, respectively. The species distributions are significantly different for adults and for juveniles with chi-square tests at $P < 0.001$.

of pahoehoe and aa lava. At points of contact between the two flows, the transition is very abrupt, occurring over a distance of 1–2 mm. The pockets, or kipukas, of the older flow vary in size from less than 1 m² to more than 10,000 m². Thus, the landscape at the site is a mosaic of the two flows.

Though both *Dubautia* species are common at the site, their local distributions differ significantly (Fig. 2, Table 2). *Dubautia ciliolata* is almost completely restricted to the older flow, whereas *D. scabra* is completely restricted to the younger flow.

TABLE 2. Distributions of adults of *Dubautia ciliolata*, *D. scabra*, and their natural hybrid at a site of sympatry on Mauna Loa, Hawaii. The site is the same as in Figure 2. The oval-shaped sample area was approximately 350 m long and 150 m wide. It included a large pocket, or kipuka, of the older lava flow that was approximately 250 m long and 50 m wide. It also included a 50-m-wide section of the younger lava flow that completely surrounded the kipuka.

Taxon	Number of adults	
	Older flow	Younger flow
<i>D. ciliolata</i>	1,692	28
<i>D. scabra</i>	0	487
Hybrid	0	29

With regard to the small proportion of adult individuals of *D. ciliolata* that grow on the younger flow, over 80% are small plants that occur within 4 m of the boundary between the two flows. In this zone, the younger flow tends to decrease in thickness. Hybrids between the two species are also common at the site. Like *D. scabra*, they are completely restricted to the younger flow (Table 2).

The differential restriction of *D. ciliolata* and *D. scabra* to the two flows occurs for juvenile and adult plants (Fig. 2), suggesting that factors leading to the differential restriction may operate primarily during the stages of seed dispersal and seedling establishment. Both species produce very large quantities of small, light, wind-dispersed seeds each year, which appear to be readily dispersed across the two flows. Hence, seedling establishment may be the more critical stage.

The local distributions of *D. ciliolata* and *D. scabra* also differ at other sites of sympatry on Hawaii. At 1,125 m near Keanakakoi Crater on the slopes of Kilauea, for example, *D. ciliolata* is restricted to a 1959 cinder substrate and *D. scabra* is restricted to an adjacent 1974 pahoehoe lava flow (L. Stemmermann, pers. comm.).

Other sympatric species in the silversword alliance also exhibit different local distributions. *Dubautia paleata* and *D. raillardoides*, for example, grow in the Alakai Swamp region of Kauai. This large, dissected, upland plateau receives 6,000–10,000 mm of rainfall per year. The vegetation is composed primarily of wet forest, with a mosaic of bogs scattered over the more level areas. Though both species are common at sites of sympatry, *D. paleata* is largely confined to the bogs, whereas *D. raillardoides* is always restricted to the wet forest (Canfield, 1986).

MORPHOLOGICAL AND
PHYSIOLOGICAL DIVERSITY

Species in the silversword alliance have a wide variety of growth forms (Table 1). All *Argyroxiphium* and *Wilkesia* species are rosette shrubs, with some species being primarily monocarpic (e.g., *A. sandwicense* and *W. gymnoxiphium*) and others being commonly polycarpic (e.g., *A. grayanum* and *W. hobdyi*). The rosettes are sessile in some species (e.g., *A. caliginis*) and elevated on woody stems up to 5 m tall in other species (e.g., *W. gymnoxiphium*). Most *Dubautia* species are shrubs, though they vary from small, spreading forms (e.g., *D. herbstobatae* and *D. scabra*) to large, woody, erect forms (e.g., *D. dolosa* and *D. plantaginea*). Three *Dubautia* species commonly grow as small trees 5–8 m tall, with the woody trunks of large individuals of *D. arborea* and *D. reticulata* reaching 0.4–0.5 m in diameter. *Dubautia latifolia* is a liana that climbs into the canopies of large trees. Stems of *D. latifolia* often exceed 8 m in length and may reach 70 mm in diameter near the base.

Species in the silversword alliance also have a wide range of leaf sizes and shapes. In the extremes, leaf lengths differ by two orders of magnitude, ranging from 5 mm to 500 mm (Table 1). All *Argyroxiphium* and *Wilkesia* species have long, narrowly ligulate to linear leaves, with the leaves of *A. caliginis* being the shortest on average. With the exception of *D. scabra* and *D. waialealae*, the 14-paired *Dubautia* species tend to have longer leaves than the 13-paired species. Leaf shapes among the *Dubautia* species include elliptic, lanceolate, linear, ovate, oblanceolate, oblong, and obovate (Carr, 1985).

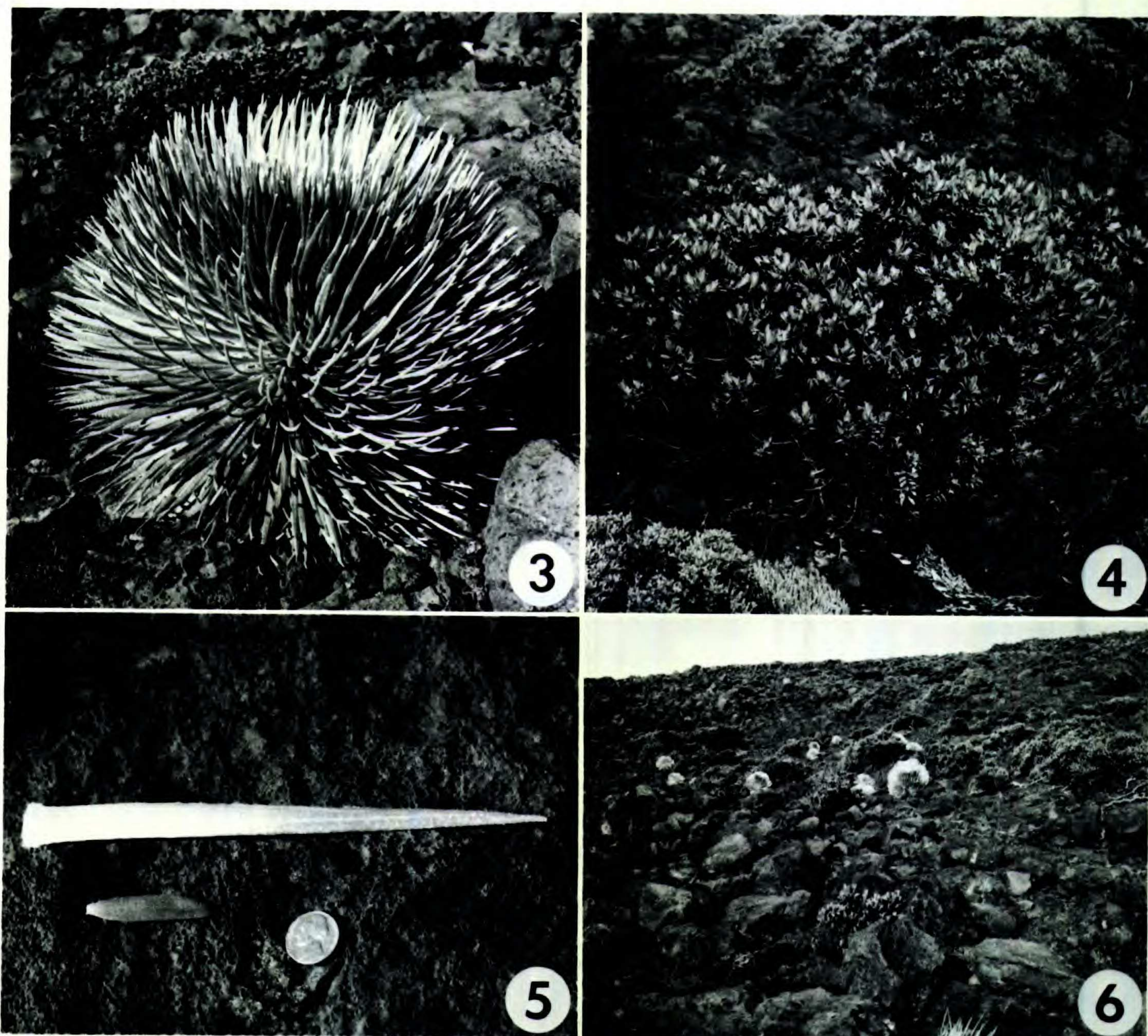
In addition to morphological diversity, species in the silversword alliance exhibit significant physiological diversity. Among the *Dubautia* species, for example, differences in chromosome number and habitat water availability are strongly correlated with differences in leaf turgor maintenance capacity (Robichaux, 1984, 1985; Robichaux & Canfield, 1985). The 13-paired species from the dry scrub and woodland habitat, such as *D. ciliolata*, *D. menziesii*, and *D. platyphylla*, have much greater capacities for maintaining high turgor pressures as tissue water content decreases than the 14-paired species from the wet scrub and forest habitat, such as *D. knudsenii*, *D. plantaginea*, and *D. raillardoides*. Their greater turgor maintenance capacities may play a key role in enabling the 13-paired species from the dry scrub and woodland habitat to tolerate conditions of low soil water availability.

Morphological and physiological diversity is also evident among species that grow in the same habitat. *Argyroxiphium sandwicense* and *D. menziesii*, for example, grow sympatrically in the alpine cinder and lava habitat of Haleakala, Maui, where environmental conditions are severe. Under the high solar irradiances characteristic of this habitat in summer, substrate temperatures are often very high during the day. Coupled with the low annual rainfall of 600–700 mm, these conditions appear to limit plant growth significantly, resulting in a landscape with very low vegetative cover.

The growth forms and leaves of *A. sandwicense* and *D. menziesii* differ significantly (Figs. 3–6). *Argyroxiphium sandwicense* is a monocarpic, rosette shrub with long, narrow, densely pubescent leaves, whereas *D. menziesii* is a polycarpic, woody, diffusely branched shrub with small, glabrous leaves. The difference in leaf pubescence results in a large difference in leaf absorptance. Leaf absorptances (0.4–0.7 μm) measured with an integrating sphere are 0.39 ± 0.01 (mean ± 1 S.E.; $N = 5$) in *A. sandwicense* and 0.80 ± 0.01 ($N = 4$) in *D. menziesii*. (The leaf absorptances are significantly different with a *t*-test at $P < 0.001$.)

The leaf water balances of *A. sandwicense* and *D. menziesii* during the middle of the summer growing season also differ significantly and are markedly influenced by the prevailing atmospheric conditions at Haleakala. On most July days, when the moisture-laden tradewinds blow from the northeast, a massive cloud bank forms around the mountain. The altitude of the cloud bank varies considerably from day to day, however, such that the atmospheric humidities to which *A. sandwicense* and *D. menziesii* are exposed also vary considerably. On 1 July 1985, for example, the upper ceiling of the cloud bank was 1,750–1,850 m throughout the day. As a result, atmospheric humidities at the study site (2,820 m) were very low, with the leaf-to-air vapor pressure gradient reaching 29 mPa Pa⁻¹ in both species at midday (Table 3). On 5 July 1985, in contrast, the upper ceiling of the cloud bank was 2,650–2,750 m during much of the day. As a result, atmospheric humidities at the study site were significantly higher, with the vapor pressure gradient reaching only 15 mPa Pa⁻¹ in both species at midday (Table 3; $P < 0.001$ for the difference between days in each species).

The large differences in vapor pressure gradients are paralleled by significant differences in leaf conductances to water vapor in both species (Table 3; $P < 0.001$ for the difference between days in each species). In *A. sandwicense* and *D. menziesii*, midday leaf conductances on 1 July 1985 were



FIGURES 3-6.—3. *Argyroxiphium sandwicense*.—4. *Dubautia menziesii*.—5. Leaves of *A. sandwicense* (upper) and *D. menziesii* (lower), with a nickel coin for scale.—6. Habitat of *A. sandwicense* and *D. menziesii* on Haleakala, Maui. For both species, the average height of mature individuals in the photograph is 0.6–0.9 m.

67.5% and 68.7%, respectively, of those on 5 July 1985. Thus in both species, a higher midday leaf conductance is correlated with a lower midday vapor pressure gradient. The correlations suggest a direct stomatal response to changes in the vapor pressure gradient, as has been reported in a large number of species from a wide variety of habitats (Schulze, 1986). Such stomatal responses enable plants to restrict water loss before severe water deficits develop.

Though the two species exhibit similar correlations between leaf conductances and vapor pressure gradients, midday leaf conductances are significantly higher in *A. sandwicense* than in *D. menziesii* (Table 3; $P < 0.001$ for the difference between species on each day). On 1 and 5 July 1985, midday leaf conductances in *A. sandwicense* were approximately twice as high as in *D. menziesii*. With its higher leaf conductances, *A.*

sandwicense also exhibits significantly higher midday and daily leaf transpiration rates than *D. menziesii* (Table 3; $P < 0.001$ for the difference between species on each day). Thus, the total daily water use per unit leaf area of *A. sandwicense* appears to be much greater than that of *D. menziesii* in July.

Despite its higher transpiration rates, *A. sandwicense* does not exhibit markedly lower midday water potentials than *D. menziesii* (Table 3). This suggests that the two species may differ in rooting depths, and thus in access to available soil water supplies. Alternatively, they may differ in hydraulic resistances or capacitances. In contrast to *D. menziesii*, *A. sandwicense* accumulates very large amounts of extracellular polysaccharide in its mature leaves (Carlquist, 1957; Carr, 1985). In the related species, *A. grayanum*, the presence of this polysaccharide is correlated with a large increase

TABLE 3. Water and temperature balance parameters of *Argyroxiphium sandwicense* and *Dubautia menziesii* on 1 and 5 July 1985 at a site of sympatry on Haleakala, Maui. The site was located at 2,820 m along the summit road. Clear skies prevailed at the site on both days, with midday solar irradiances exceeding 1,020 W m⁻². Standard errors of the means are given in parentheses. Results of the relevant *t*-tests are provided in the text.

Parameter ¹	<i>A. sandwicense</i>		<i>D. menziesii</i>	
	1 July	5 July	1 July	5 July
Midday vapor pressure gradient (mPa Pa ⁻¹)	29.1 (0.1)	15.5 (0.1)	29.1 (0.4)	15.3 (0.3)
Midday leaf conductance (mmol m ⁻² s ⁻¹)	332.7 (4.5)	493.1 (4.3)	170.0 (11.6)	247.6 (7.8)
Midday leaf transpiration rate (mmol m ⁻² s ⁻¹)	8.7 (0.1)	6.6 (0.1)	4.7 (0.3)	3.5 (0.1)
Daily leaf transpiration rate (mol m ⁻² d ⁻¹)	276.2 (5.1)	234.8 (4.1)	158.0 (12.4)	113.3 (4.2)
Midday water potential (MPa)	-1.1 (0.1)	-0.9 (0.1)	-1.0 (0.1)	-0.8 (0.1)
Midday leaf temperature (°C)	19.6 (0.1)	17.7 (0.1)	19.5 (0.2)	17.6 (0.2)

¹ Parameters were measured for five individuals per species, with the ten individuals growing intermingled in an area of approximately 10 m radius. Except for water potentials, parameters were measured for 2–4 recently mature leaves per individual. Leaf and air temperatures were measured with 0.127-mm copper-constantan thermocouples connected to a Wescor Corp. model TH-65 digital thermocouple thermometer. Leaf conductances to water vapor were measured with a LI-COR Corp. model LI-1600 steady-state porometer. Both species were amphistomatous, with the upper and lower leaf surfaces contributing approximately equally to the total leaf conductances. In *A. sandwicense*, the measured leaf conductances included the effects of the dense, appressed pubescent layer. Leaf conductances were measured at 2–3-hr. intervals throughout the day, with each measurement sequence taking 0.3–0.7 hr. Midday leaf conductances were the maximal leaf conductances in both species. Boundary layer conductances to water vapor and leaf transpiration rates were calculated according to the equations in Nobel (1983). Wind speeds were measured with a hot-wire anemometer and averaged 1 m s⁻¹ during the sampling periods. Atmospheric humidities were measured with the humidity probe in the porometer. Intercellular-air-space humidities were assumed to be saturated and were calculated from the measured leaf temperatures. Estimates of daily leaf transpiration rates were obtained by integrating the diurnal curves for each species. Hydrostatic pressures in the tissue apoplast were measured with a PMS Inst. Co. model 600 pressure chamber fitted with a 0–3-MPa, 150-mm-diameter gauge. The hydrostatic pressures in the tissue apoplast were assumed to equal the water potentials in the tissue symplast (Koide et al., 1989). Measurements were made on the terminal 130 mm of recently mature leaves of *A. sandwicense* and on terminal shoots of *D. menziesii*.

in leaf capacitance (Robichaux & Morse, 1990).

The midday temperatures of recently mature leaves of *A. sandwicense* and *D. menziesii* in July do not differ significantly (Table 3). Both species exhibit leaf temperatures of 17–20°C, which is quite moderate given that midday solar irradiances at the study site in July typically exceed 1,020 W m⁻², while midday substrate temperatures exceed 55°C. Thus, recently mature leaves of *A. sandwicense* and *D. menziesii* appear to be equally effective at decreasing heat energy inputs and increasing heat energy outputs. In *A. sandwicense*, steep leaf angles and low leaf absorptances (Figs. 3, 5) may aid in decreasing inputs, while high leaf transpiration rates (Table 3) may aid in increasing outputs. In *D. menziesii*, steep leaf angles (Fig. 4) may aid in decreasing inputs, while small leaf sizes (Fig. 5) may aid in increasing outputs.

In marked contrast to recently mature leaves,

young leaves of *A. sandwicense* experience very high temperatures for a significant portion of the day (Fig. 7). The young leaves are located at the bottom of the cone-shaped depression in the center of the rosette. During the early morning, when the young leaves are shaded from direct solar irradiance, their temperatures are lower than those of the exposed, recently mature leaves. Once direct solar irradiance penetrates the cone-shaped depression, however, the young leaves experience a rapid increase in temperature and reach maximal temperatures in excess of 37°C by early afternoon. In *D. menziesii*, which lacks the rosette growth form, midday temperatures of young and recently mature leaves are not significantly different.

Argyroxiphium sandwicense and *D. menziesii* thus illustrate the contrasting modes of morphological and physiological adaptation that have evolved within the silversword alliance. Though the

two species grow in the same habitat, they exhibit different suites of traits enabling them to cope with the severe environmental conditions.

ADAPTIVE RADIATION

The ecological, morphological, and physiological diversity of species in the silversword alliance is exceptional. The patterns of diversity and genomic relationships among the species suggest that a variety of factors may have played important roles in their adaptive radiation.

First, the periodic origin of new islands in the archipelago may have offered repeated opportunities for interisland dispersal and colonization. At least fourteen major dispersal and colonization events appear to have occurred during the evolutionary history of the silversword alliance (Carr et al., 1989). Founder effects associated with these events may have resulted in the evolution of new morphological and physiological traits.

Second, the wide variety of habitats and wide range of elevations in the archipelago may have facilitated rapid ecological divergence, which is evident in the modern species at grand and local scales. Rapid divergence may have been further enhanced by a genetic system that allowed for a high degree of morphological and physiological flexibility. Striking evidence for such flexibility is provided by *A. sandwicense* and *D. menziesii*, two species that differ radically in morphology and physiology, yet readily produce vigorous, fertile hybrids in nature (Carr & Kyhos, 1981).

Third, chromosomal repatterning at the diploid level may have promoted reproductive isolation between species and may have contributed to the origin of novel gene complexes. Based on cytogenetic evidence, at least eight major genomic arrangements exist among species in the silversword alliance (Carr & Kyhos, 1986; Carr et al., 1989). The genomic arrangements are structurally differentiated via reciprocal chromosome translocation or aneuploid reduction. The degree of postzygotic reproductive isolation between species, as measured by the pollen stainability of hybrids, is strongly correlated with the degree of chromosomal differentiation. With respect to the origin of novel gene complexes, the aneuploid reduction in chromosome number among the *Dubautia* species is correlated with several major ecological, morphological, and physiological differences. Relative to the 14-paired *Dubautia* species, the 13-paired species extend into drier environments, have smaller leaves, and have greater turgor maintenance capacities. Thus, the aneuploid reduction in chro-

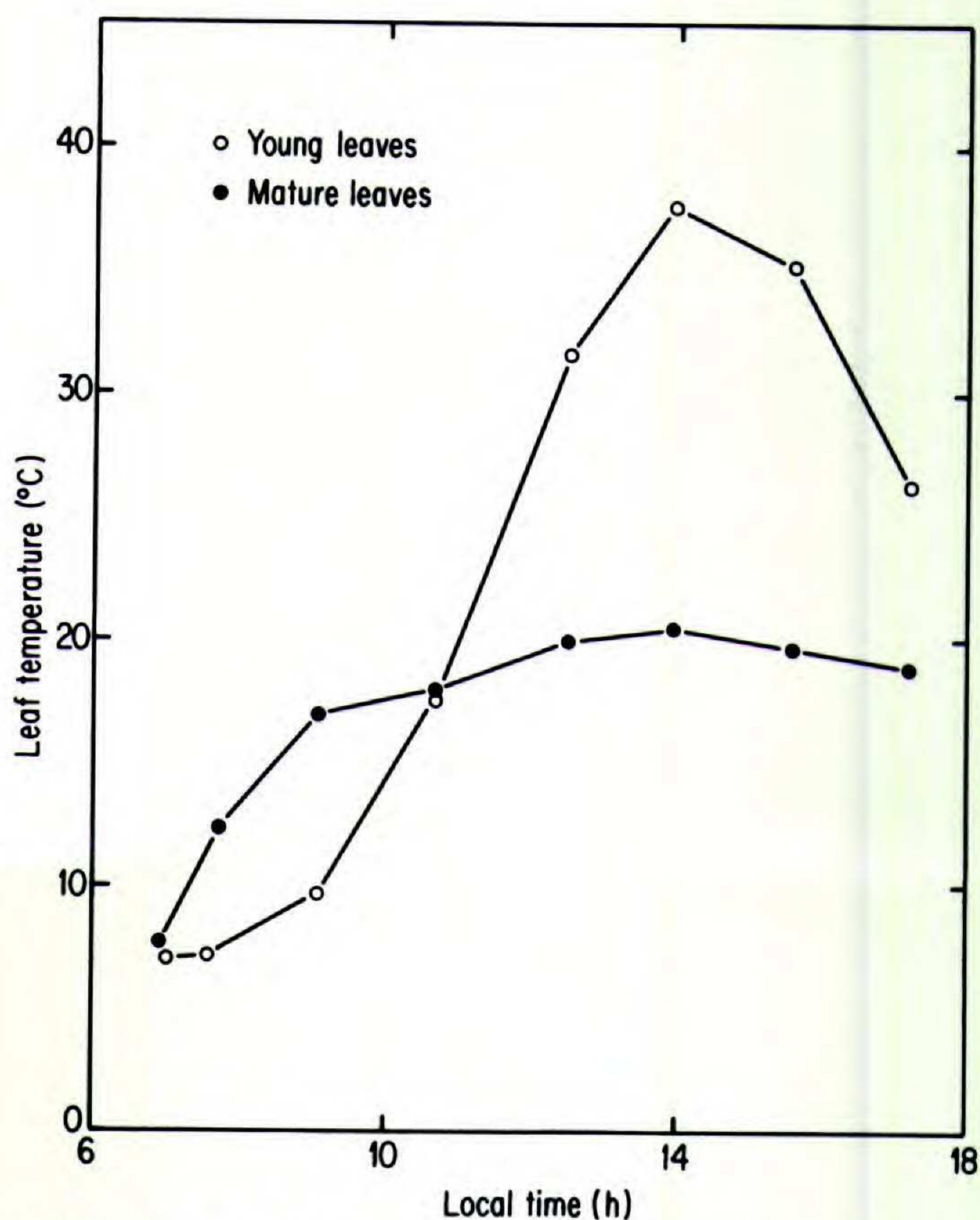


FIGURE 7. Temperatures of young and recently mature leaves of an individual of *Argyroxiphium sandwicense* on 18 July 1982 on Haleakala, Maui. Young leaves were less than 40 mm long. Air temperature was 7.4°C at 0700 hr. and 19.2°C at 1400 hr. Midday solar irradiance exceeded 1,020 W m⁻². At 1400 hr. on 2 July 1985, young and recently mature leaves of six individuals of *A. sandwicense* had temperatures of 40.6 ± 0.4°C and 20.2 ± 0.4°C (mean ± 1 S.E.), respectively. The leaf temperatures on 2 July 1985 are significantly different with a *t*-test at *P* < 0.001. The site and measurement techniques were the same as in Table 3.

mosome number may have been particularly important in the evolutionary history of the silversword alliance.

Understanding the specific roles played by these and other factors in the adaptive radiation of the silversword alliance will require more detailed analyses. Whatever their roles, it is clear that their combined effect has resulted in an extraordinary degree of diversification.

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